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Skull growth in equids beyond domestication

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Abstract

The size of body parts often co-vary through exponential scaling, this is known as allometry. Allometric changes are important to the generation of morphological diversity. To make inferences regarding the evolved responses in allometry to artificial selection in the genus *Equus*, we compared allometric parameters (slope and intercept) among 18 domestic breeds (11 for horses and 6 for donkeys) and 7 wild species, attempting to interpret the differences in allometric parameters (body length, withers height and head length). The allometric values were not different among domestic equids. Breeds of similar sizes have similar head lengths. The elongation of head length is related to overall body size, indicating that allometry was invariant and did not change under specific selection in the breed formation. Head elongation (dolicocephaly) is probably focused on the preorbital region (dolicoprosopial) rather than on basicranial region. A remarkably higher correlation among donkey breeds can be explained by its strong similar morphological evolution. These findings provide evidence that changes in the allometry pattern point to modifications of ontogenetic processes derived from breeds differentiation and evolution. Further analysis should focus on the relationship between ancestral ontogeny and adult morphology in equids.

Introduction

Animals are not isometric; that is, their organs generally do not scale in a linear fashion with their bodies [1]: as they increase in body size, they tend to change the proportions of various body parts relative to the body as a whole [2]. The term 'allometry', in its broadest sense, designates the differences in proportions correlated with changes in absolute magnitude of the total organism or of the specific parts [3]. Allometric differences, particularly those among closely related species, often directly relate to performance requirements [2]. For example, a large animal requires proportionately thicker limbs to support its body mass compared to a smaller animal [2]. In this simple case, allometric variation is accounted for by general scaling laws, because limb cross-sectional area, the biomechanically important parameter for limb strength, scales to body mass$^{2/3}$. In other cases, it is more difficult to directly relate allometry to organismal performance. This is particularly true for structures, such as the cranium, that have multiple functions [2]. In fact, the skulls offer a morphological diversity, given its complexity in form (shape and size) and embryological origin (mesodermal and neural crest; pharyngeal arches, dermatocranium and endocranium, and its relation to organs such as the brain, to sensory organs and to feeding function [4]. In such cases, the significance of allometry could be investigated by examining how allometric variation impacts variables that may be important for organismal performance, such as those related to feeding [2].

Many morphological traits are strongly correlated with body size through scaling relations that often follow the power law, $Y=aX^b$, where Y represents a body part, X represents another part or the whole, and a and b are constants [5]. This equation commonly employs not this linear but a log-log scaling, where the relationship becomes linear [5], $\log Y=\log(a) + b \log X$ (Kruska 1988). The slope, b, is the "proportionality constant" [1] or "allometric coefficient" and its constancy indicates that the ratio between the rates of growth in Y and X remains unchanged [6]; the constant a is the Y value at X=1, which is often outside the range of the data being collected [6]. Moreover, the value of a is changeable depending on the choice of units for X and Y; thus, this variable has received less attention because its significance is difficult to interpret. However, it has been emphasised the significance of the allometric intercept in ontogenetic and phylogenetic changes and as a taxonomic indicator [6]. Size differences occur in ontogeny, phylogeny, or arise merely from the static comparison of related forms at one growth stage (usually the adult) [3]. Ontogenetic, static, and evolutionary allometries are recognized depending on whether the relationship between a trait and its size is taken during the growth of an individual, across individuals measured at similar developmental stages between the means for populations or species [5]. A common interpretation of the ontogenetic and static allometric slopes has been that they represent a ratio of proportional growth between the trait and overall size [5].

Researchers studying allometry in animals have usually attempted to relate the size of the organ to some functional property of that organ [1]. It is reported that there exists a common allometric pattern across mammalian taxa, in which small species possess proportionally shorter faces and wider braincases than large species [7]. This trend has been called the cranial evolutionary allometric (CREA) 'rule' [7].

The equids experienced various forms of natural and artificial selection through adaptation to a diversity of environments before their domestication and subsequent breed improvement. In the present study, we statistically compare allometric parameters (slopes and intercepts for head length to body length and withers height) for various types of domestic and wild equids using ontogenetic data collected from bibliographical sources. We then attempted to interpret the differences in relation to their courses of differentiation, evolution and breed improvement to make inferences regarding the evolved responses in ontogenetic allometry to natural and artificial selection.

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Materials and methods

Data collection

To compare allometric relationships among breeds, paired measurements of body length (BL), withers height (WH) and head length (HL) were collected for the following extant breeds of equids (the family Equidae): 5 horses, 6 ponys (considering ponys those with less than 141 cm in WH), 6 donkeys, and 7 wild species belonging to the genre *Equus* (Table 1). Data for all animals were collected from literature (see References). Descriptive statistics of the data sets used for the analyses are provided in Table 1. Only data from male animals were considered in this study.

Statistical analyses

The bivariate allometry relating HL to WH and to BL was analysed according to the allometric equation $Y=a\ X^b$, where Y=dependent variable, and X=independent variable. Taking the natural logarithm of both sides, the equation was linearly transformed: $\log Y=\log(a) + b \log X$. This bivariate approach is suitable for statistical comparison of slopes and intercepts of regressions for wild versus domestic forms (Sánchez-Villagra *et al.* 2017) [4]. All of the data were fitted in the equation via the ordinary least squares with data log-transformed. Comparisons of slopes were done by an ANCOVA test. Analysis were done using the PAST software [21]. The present statistical analyses ignored phylogenetic relationships between breeds due to lack of appropriate resources, and therefore there is the possibility that the differences across them might be overestimated.

Result

The allometric parameters for breed comparisons are presented in Table 2. Among groups, donkeys presented a linear regression closer to isometry (r=0.967 and 0.973 for WH and BL respectively) than the rest (Table 2). The mean slope for overall species/breeds was -0.059. The allometric slopes did differed between groups, both for WH to HL (p=0.017) as for BL to HL (p=0.038), whereas no significant differences were found among domestic breeds (p>0.05), for which there were homogeneous slopes (F>0.4, p>0.2), for both traits. Strong negative correlation (r=-0.994 and -0.989, p<0.05 for WH and BL respectively) was observed between slope and intercept across the species and breeds, indicating that the intercepts were affected by the slopes. From the regression coefficient between slope and intercept, the allometric lines came close to intersecting at WH=84.1 cm and BL=87.2 cm for domestic breeds, and at WH=84.1 cm and BL=594 cm for wild *Equus*. The intercepts for BL o HL of wild *Equus* were higher than those of all of the other traits and groups.

Table 1. Descriptive statistics (wither height, body length and head length, in cm), of the data sets used for the analyses

Species/breed	Withers height	Body length	Head length	Source
Andalusian donkey	150.3	148.4	65.2	[8]
Andalusian horse	155.6	154.6	58.9	[9]
Araucano	133.0	130.8	54.4	[10]
Campeiro horse	145.0	147.0	55.0	[11]
Catalan donkey	141.3	144.1	60.9	[8]
Chileno	140.3	144.8	54.1	[12]
Chilote	121.0	126.0	42.0	[12]
Czech donkey	109.9	113.3	44.4	[13]
Donkey from Encartaciones	114.2	118.5	51.6	[8]
Equus asinus	125.0	200.0	43.4	[14]
Equus burchelli	231.5	127.5	49.3	[14]
Equus grevyi	152.5	135.0	59.7	[14]
Equus hemionus	120.0	221.0	48.2	[14]
Equus kiang	210.0	210.0	50.4	[14]
Equus przewalskii	138.0	260.0	48.2	[15]
Equus zebra	133.0	220.0	53.6	[14]
Galego pony	119.0	129.0	51.0	[9]
Majorcan donkey	136.4	139.3	60.5	[8]
Majorcan horse	161.8	160.2	62.3	[16]
Pantaneiro horse	146.1	146.2	62.2	[17]
Pottoka pony	125.6	129.9	56.9	[18]
Pyrenean Catalan Horse	154.2	169.2	61.2	[19]
Terceira pony	129.7	128.0	49.1	[20]
Zamorano-leonés donkey	139.3	140.0	60.4	[8]

Table 2. Regression coefficients, slopes and intercepts for withers height and body length to head length, for the breeds/species comparisons. Significant differences appeared in wild forms, but no significant differences were found among domestic breeds (p>0.05)

	Withers height			Body length		
	r	Slope	Intercept	r	Slope	Intercept
Horses	0.510	0.221	0.502	0.432	0.136	0.966
Ponys	0.487	0.319	-0.102	0.494	0.374	-0.574
Donkeys	0.967	0.462	0.000	0.973	0.519	-0.888
Wild *Equus* species	0.178	0.012	1.550	-0.428	-0.045	2.062

Discussion

Horses were probably first domesticated roughly by 3,500 BC [22], somewhere in the steppes of modern-day Ukraine and Kazakhstan, the main distribution area of wild horses at the time of domestication [23]. Donkeys were domesticated in modern-day Syria, Iran, and Iraq dating to ca. 2,800–2,500 BC [24]. Most of the breeds of equids examined in the present study diverged probably centuries and have sizes and shapes adapted to the environment in different ways under natural and artificial selection. From their formation to the present, these breeds have been continuously and strongly selected by humans for the purpose of improving desired traits.

Mammals have changed over long periods of time as a consequence of domestication [25]. The investigated species and breeds have similar trajectory patterns among them. Constant allometric slopes have been interpreted as the result of invariant growth regulation mechanisms (CREA hypothesis). But the changes in trajectories recorded in wild versus domesticated forms are not equal, so there is a certain commonality in *Equus* domestication. Isometric growth implies that two individuals of different size basically look alike [4]. Only isometry of donkeys is corroborated here. The isometric growth of donkeys would be explained, at least in part, by the relative conservatism in this species when compared with horses. For the rest of domestic *Equus* there appeared only allometric changes. This large amount of allometric change in horses and ponys suggest an intrinsic propensity for change -even with minor changes in size- [4].

Hypotheses to explain evolutionary, cross-species, allometries fall in two broad classes: those based on functional adaptation between traits and those based on developmental constraints on the evolution of the traits [5]. The intercept independent of the slope is difficult to alter over a short time; therefore, based on the detected conservatism (e.g. similar intercepts) of studied domestic forms, and the universal patterns of allometric or isometric growth for some of the skull parts in the wild and domesticated species [4], allow us to conclude that evolutionary allometries in *Equus* formation of breeds has arisen by a mere selection on body size, not in head size. Because although it is well established that during growth the neurocranial components of the skull, mostly related to the brain and sensory organs, scale negatively whereas the splanchnocranial components, related to the masticatory apparatus scale positively with size [4], our data include "head length", so with no differentiation between neurocranium and splanchnocranium.

Voje *et al.* [5] estate that most quantitative traits are highly evolvable and respond rapidly to both artificial and natural selection. Detected morphological allometric patterning in domestic *Equus* forms is explained as a by-product of selective constraints associated with size change. That is, head morphology would be constrained by developmental boundaries, reflecting alterations produced by strong selection for size. Domesticated *Equus* forms have growth trajectories different from their respective wild counterparts with regard to the slopes, as previously stated in other species by other authors [4,26]. This head elongation would probably be explained by a facial (e.g. splanchnocranium) rather than a cranial (e.g. neurocranium) elongation. In other terms: according to an increase in size (both as body length as withers height), dolicocephaly (head elongation) is expressed as dolicoprosposy (preorbital -cheek and muzzle- elongation).

Experiments on artificial selection of wing shape or wing-body size scaling in fruit flies demonstrated that the static allometric slope could be altered within several generations, but that the response was rapidly lost when selection was suspended [27]. So, the similarities in slopes found in the present study may also be the recent result of specific similar artificial selection, far from the beginning of the domestication. We are talking about the selection based on "pedigree breeds" (that began in England in the mid to late 1700s, pioneered by Robert Bakewell) [28]. Moreover: in the present analysis, the original intercepts (log(a)) were strongly affected by the slopes (e.g. a high dependence from the slopes), thus a fair comparison of the intrinsic difference in allometric intercept (i.e., proportional shift in the size of Y relative to X) would not be possible. I.e.: the observed similarities in the intercept among domestic forms may be explained by the morphological phylogenetic changes occurring on micro time scales, that is, the "pedigree breed formation" period.

Conclusion

Our comparative analysis of allometry between head length and body length and withers height across breeds of domestic equids suggest that the allometric slope is typically invariant among breeds and it has not been changed although strong, specific selection, between horses, ponys and donkeys. These implications will be helpful for obtaining a deeper understanding of evolved responses in allometry for domestic *Equus*.

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